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PROBABLE RELATIONS OF CLIMATIC CHANGE TO THE ORIGIN OF THE TERTIARY APE-MAN

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THE geologic record not only contributes the testimony of fossils to the evidence of the course of organic evolution, but, when the nature of the enclosing rock is interpreted, a knowledge is reached of the environment of the ancient organisms as well; whether of the sea, lake, marsh, river or desert in its conditions. A feature of ancient environments to which increased attention has been given in the past two decades is that of climate and its variations. In terrestrial life it is the most fundamental factor. Especially in the Pleistocene, the faunas are seen to have come and gone at the command of climatic change. Those animals which were trapped on the northern sides of mountain ranges or water barriers were remorselessly exterminated by the waves of advancing cold: those which could escape to the south returned with milder climates, but changed in their assemblage. The Pleistocene is so near and its climatic oscillations are so conspicuous by virtue of its record of continental glaciation still existing around us on the surface that its climatic importance in faunal changes is freely recognized; but what of the more and more remote geologic periods? Even when there is no record of glaciation there are in many cases evidences recorded in the solid rocks of oscillation from optimum life conditions toward either cold or aridity; and high aridity, spreading deserts far and wide, produces changes as profound as does the culmination of cold in glaciation. What correlation can be drawn between these earlier and less known climatic changes and those modifications of the faunas which are expressive of progress in evolution, marked by the initiation of new modes of life?

In connection with the teaching of historical geology, this subject of ancient climates and their relations to evolution in the vertebrates from fish to man has been held in mind by the writer for more than a decade. In sequence to earlier papers on the physical side of these problems, one was recently published on "The Influence of Silurian-Devonian Climates on the Rise of Air-breathing Vertebrates,"[1] and the conclusions reached in that paper form the basis of a parallel argument for this.

An outline of that argument on the causes leading to the origin of air-breathing vertebrates is as follows: The geologic evidence on the nature of the physical environment in Silurian and Devonian times, combined with the fossil record and supplemented by the archaic vertebrates which still linger in life, indicates that recurrent epochs of semi-aridity brought conditions of severe repression upon river fishes. As the dry season advanced the rivers were reduced in flow, the content of oxygen decreased and the extreme restrictive conditions were represented by isolated pools, stagnant and foul from the decomposition of animal and plant remains. The piscine fauna which endured these conditions came through profoundly changed. The primitive sharks found earlier in fresh-water deposits, having no air-bladder, were driven to the seas. The fresh-water fishes which remained were ganoids and dipnoans, fishes with air-bladders efficient for the direct use of air. Finally, from crossopterygian ganoids, under the stimulus of the semi-aridity of the Devonian, there emerged the amphibians; able to carry forward their activities as terrestrial animals. This was a major step in the remote evolution of man.

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[1] Joseph Barrell, *Bull. Geol. Soc. Am.*, Vol. XXVII., 1916, pp. 387–436, abstract in *Proc. Nat. Acad. Sci.*, Vol. II., 1916, pp. 499–504

Did a similar climatic change in the Tertiary period acting on a species of large-brained and progressive anthropoid apes isolated from the regions of continued forest compel them to adapt themselves to a terrestrial life or die? Did the gradual dwindling, leading even to the extermination of forests, in a region from which the forest fauna could not escape, produce a rigorous natural selection which transformed an ape, largely arboreal and frugivorous in habits, into a powerful, terrestrial, bipedal primate, largely carnivorous in habit, banding together in the struggle for existence and by that means achieving success in chase and war? The gradual elimination, first of the food of the forests, lastly of the refuge of the trees, through increasing semi-aridity, would have been a compelling cause as mandatory as the semi-aridity which compelled the emergence of vertebrates from the waters, transforming fishes into amphibians; the first of the vertebrate rulers of the land.

It is the purpose of the present article to assemble the evidence which suggests this climatic cause acting upon our simian ancestors as a controlling factor in this latest of the major stages in human evolution. It falls into accord with the general conclusion of Matthew that "the evolution of land life in adaptation to recurrent periods of aridity supplies a satisfactory background of cause for the whole evolution of the higher vertebrates."[2] The writer also has had the advantage of discussing this subject with Professor R. S. Lull, whose large knowledge of the organic side of these problems has served as a source of reference and has been in many ways of special value.

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[2] W. D. Matthew, "Climate and Evolution," *Annals of the New York Academy of Sciences*, Vol. XXIV., 1915, pp. 171–318 (p. 181).

The significance of evidence depends largely upon the hypotheses which control its interpretation. For that reason, before taking up the facts which bear directly upon the adaptation of man to a terrestrial habitat, there should be considered the general relationship of environment to evolution.

The changes in successive faunas prove that internal factors modify the strains of heredity and that new species thereby become established, even though there are at present large differences of opinion in regard to the mode of operation of those internal factors. On the other hand, the general adjustments of organisms to environment, as marked by their efficiency in meeting the conditions around them, prove also that evolution is correlated and conditioned in some way with environment. There is then a complex of actions, interactions, and reactions, both within and without the organism; such as Osborn has emphasized.[3] Nevertheless, in the complex of actions and reactions which accompany organic progress, there must be in each step some leading cause; the others follow. The evidence from the geologic record, when combined with the biologic evidence derived from the study of living organisms, seems to show that the great upward steps in evolution are primarily determined by environmental changes which operate to diminish the quantity of life and work toward the extinction of ancient types.

On the other hand, in the splitting of a family into various subfamilies, genera and species, the leading rôle would seem to be taken by a tendency toward organic change, the environment remaining in the meantime nearly constant. The tendency to organic change—variation, mutation, or whatever it may prove to be—is apparently often manifested, when once started, by a progression in one direction, indicating the acquisition of an evolutionary momentum known as orthogenesis. The lines of orthogenetic progress must not transgress flagrantly, however, the limits of efficiency; since in that event natural selection will begin to operate and terminate the line. That environment and natural selection are not the initial or controlling causes in such orthogenetic changes is suggested by the fact that differences arise which are immaterial to the environment and in many cases progress considerably beyond the limits of efficiency before the law of the survival of the fittest emerges into operation.

Naturalists have often in their mental pictures simplified nature too much and made a single cause too inclusive in its action. They have often also not given heed to the indications that different kinds of evolution have been due to a different category in the controlling cause. The early advocates of the doctrine of descent made everything dependent upon the influence of natural selection as the mainspring of evolution. On the other hand, it would appear that many who have studied modern organisms, but who have not weighed fully the geologic evidence, have been too sweeping in their conclusions that the Darwinian explanation of the mode of evolution must be more or less wholly supplanted by some other mode. To state or imply, as some students of Mendelianism have done, that the evolution from protozoan to higher metazoan has been determined by the mere continued dropping away of inhibiting factors seems an extremely narrow and partial view, overlooking causes, and mistaking mere mechanistic modes of internal reaction for the whole of a complex series of actions, interactions and reactions.

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[3] H. F. Osborn, "The Origin and Evolution of Life Upon the Earth," THE SCIENTIFIC MONTHLY, p. 10, July, 1916.

Bearing in mind this cooperation of various factors in organic evolution, let us turn to that last great step in human evolution, the transformation of the arboreal ape to a ground-dwelling ape-man, maintaining himself in contest with the powerful foes which were previously rulers of the ground. We must note first that most evolutionary studies deal primarily with the anatomical characters and phylogenetic relationships. In so far as the environmental setting of the evolutionary changes is concerned, the tropical forests of southeastern Asia have been favored as the original home of man. The discussion of the causes of this evolution have generally been secondary, the conventional hypothesis holding that a tropical man-ape in the forests of southeastern Asia left the sheltering trees simply because he had advanced to a certain stage where, like a child grown up, he had the ambition and found the ability to go forth and conquer a different world from that of the adolescence of his race. The alternative hypothesis which will be set forth here is, specifically, that the compulsion of increasing aridity in Miocene times, by isolating anthropoids north of the Asiatic mountain systems and reducing the forests there to savannahs and open plains, was the primary cause in the differentiation of the ape-man from the apes and thus was fundamental in the initiation of human evolution. This hypothesis is in accord with the views of Matthew in regard to the conditions surrounding the center of dispersal of man. Matthew has stated:

> In view of the data obtainable from historical record, from tradition, from the present geographical distribution of higher and lower races of men, from the physical and physiological adaptation of all and especially of the higher races, it seems fair to conclude that the center of dispersal of mankind in prehistoric times was central Asia north of the great Himalayan ranges, and that when by progressive aridity that region became desert it was transferred to the regions bordering it to the east, south and west. We may further assume that the environment in which man primarily evolved was not a moist or tropical climate, but a temperate and more or less arid one, progressively cold and dry during the course of his evolution. In this region and under these conditions, the race first

attained a dominance which enabled it to spread out in successive waves of migration to the most remote parts of the earth.[4]

To present the data on which the present hypothesis rests, let us examine the geologic and climatic changes over Asia during the Tertiary period.

In the Eocene the ancient Mediterranean of Tethys still existed as a shallow sea stretching through Eurasia along the belt of the present Alpine-Himalayan mountain systems. As shown by both floral and faunal evidence, warm and moist climates prevailed over the earth, outside of the tracts of tropic deserts determined by the planetary winds. Some variation of climates is evident, as shown, for instance, by glacial deposits in the early Tertiary of Colorado, but, especially during the middle and later Eocene, subtropical forests existed widely over the north-temperate zone.

Similar climatic conditions characterized the Oligocene, a warm temperate flora occurring in Greenland and palms in the region of the Baltic; but on the whole the climates were somewhat cooler than in the Eocene and more variable. The flora indicates a lessening of humidity and a clearer differentiation of the seasons. The first movements of uplift began to be felt in the Pyrenees and along the Alpine trough.

The Miocene was marked by a great crust movement which separates the younger from the older Tertiary. The floor of Tethys was now compressed, the shallow sea displaced, subsidence gave place to uplift, and the greatest mountain system of the globe began to grow through vast repeated movements in the crust. The continents also were elevated and widened, connections established, and intermigrations of previously isolated faunas took place. The forest-dwelling types became restricted, largely exterminated, and animals of the plains in the form of horses, rhinoceroses and the cloven-footed mammals greatly expanded in numbers and in species. This profound faunal change implies drier climates and is in harmony with the implications of the growing mountains. There was now a lesser area of tropic seas to give moisture to the atmosphere. The mountains were now effective barriers shutting off the moisture-bearing winds from the interior of the continents. Marine invertebrate faunas indicate cooler and more zonal climates, a result, perhaps, of a less free oceanic circulation.

These climatic effects in the Miocene were moderate in amount so far as the chilling was concerned, with the result that a great expansion of mammalian life took place and it was not until the close of the Pliocene that animals of temperate climates were much restricted in their migration across the Alaskan land bridge between Asia and North America.

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[4] W. D. Matthew, "Climate and Evolution," *Annals New York Acad. Sci.*, Vol. XXIV., p. 212, 1915.

The Pliocene differs from the Miocene in the gradual advance of more temperate conditions in the middle temperate zone and of rigorous climates in the higher latitudes.

Let us turn to the history of primates in relation to this succession of Tertiary geographies and climates. We may use for this purpose the recent comprehensive phylogenetic studies of W. K. Gregory of the American Museum of Natural History.[5]

The anthropoid apes make their first appearance, so far as now known, in the lower Oligocene Fayûm deposits of Egypt. *Propliopithecus* occurs there, a very primitive but true anthropoid. This is a region where the Ethiopian and Eurasian faunas mingled and the apes clearly belong to the latter. During the course of the Oligocene the wide extent of tropical and subtropical forests throughout Eurasia must have given the primates opportunities for a wide expansion north and south, with a corresponding increase in numbers and diversity of species. Our knowledge of fossil remains is a blank, however, until the upper Miocene, at which horizon *Pliopithecus,* an ancestral gibbon, has been found in Europe. At about the same geologic level, in the Lower Siwaliks of northern India, have been recovered the fossil fragments of a number of genera. Of these, *Paleosimia* is an ancestral orang. *Sivapithecus,* according to Gregory, stands between the line of the orang and that of the *Hominidæ* but is not ancestral to either. *Dryopithecus,* which is represented by six species, three from the Siwaliks and three from Europe, stands close to the ancestral line of the gorilla and chimpanzee. After the lower or possibly upper Pliocene, no fossil remains of primates have been found until the Pleistocene. Here the human record begins and is more abundant than that of the apes. Most unexpectedly, however, a jaw of a chimpanzee has been unearthed from the Pleistocene of England in association with the Piltdown human cranium, *Homo dawsoni.* The occurrence in fact was so unexpected that the discoverers of the cranium regarded the jaw as belonging to the same individual. The careful anatomical study by Miller,[6] however, seems to show that the remains of a chimpanzee had accidentally become mixed in the same deposit with the remains of man. This evidence indicates that for a long period in the later Tertiary the anthropoid apes were capable of expansion under favorable conditions, and that on the contacts of the early human and the simian environments the two could be found in association. It emphasizes also the fact that active arboreal animals only by the merest chance give rise to fossils and may extend over a wider range of time and space than would be indicated by the recovery of their remains.

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[5] "Studies on the Evolution of the Primates," *Bull. Amer. Museum of Nat. Hist.,* Vol. XXV., Art. XIX., pp. 239–355, 1916.

[6] Miller, G. S., "The Jaw of the Piltdown Man," Smithsonian Misc. Col., Vol. 65, No. 12, pp. 1–31, pls. 1–5.

In deposits of early to middle Pleistocene age the remains of man have been found in widely separated localities: *Pithecanthropus erectus* in Java, *Homo dawsoni* in England, *Homo Heidelbergensis* in Germany. By the time of the early Pleistocene the body of the *Hominidæ* was, however, about as well adapted to ground-dwelling as at present, as seen in the femur of *Pithecanthropus*. In the Neanderthal man of the Upper Pleistocene the form of the foot and the relative proportions of leg and arm show that man had already been a terrestrial animal for at least a geologic epoch. The jaw and teeth of the Heidelberg man show the possession of clearly human though very primitive characters, a complete change from the dental type of apes adapted to a frugivorous diet. As pointed out by W. K. Gregory, although the canines have diminished in size, the erect incisors, with an edge to edge bite, are well adapted for the biting and tearing off of flesh, and the powerful jaws were capable of crushing small bones. With the use of crude weapons for the killing of animals the modifications in teeth and jaws represent a carnivorous-omnivorous adaptation fully worked out in a terrestrial and predatory primate. Thus both in dispersal and terrestrial adaptation, as seen in the early Pleistocene, there is evidence that the origin of man goes back to a far more remote period of time. It appears probable, therefore, that this adaptation goes back to the Miocene. It is possible, so far as the fossil evidence is concerned, and leaving aside the problematic evidence of Pliocene eoliths, that the adaptation to the ground may have occurred in the early Pliocene, but the experience of paleontologic discovery indicates that the initiation of new adaptations usually goes back a considerable distance in time beyond their perfection and the resulting dominance of the possessors.

Assume, then, as probable, that by the early Miocene the differentiation of anthropoids had given rise to forms resembling somewhat the chimpanzee. This line of large-bodied, intelligent, and somewhat gregarious apes, though chiefly arboreal, would have possessed some agility on the ground. We may grant them also some degree of cooperation in hunting small animals, and in fighting they may have used sticks or stones as weapons. But such apes, even if thus progressive, would still have been at the mercy of the wolves and great cats unless they remained within reach of their refuge in the trees. The greater part of their diet must still have consisted of fruit, succulent vegetation, insects, young birds, and birds' eggs. Such a beginning was still far removed from independence from the trees, both for food and refuge. The limb structure must still at that time have been adapted for arboreal life with resulting inefficiency for a terrestrial habitat. The mentality must still have been far below that level of cunning, resourcefulness, cooperation, and courage necessary for the maintenance of apes of generalized form in competition with the powerful terrestrial fauna.

How was this step taken which transferred the habitat and transformed the quadrumanous arboreal man-ape into a bipedal terrestrial ape-man, standing nearly erect and facing the dangers of the ground? As noted previously, two answers may be made. The conventional one has been that organic advancement without calling upon any changes in geography or climate gradually adapted the ancestors of man to live more or less freely upon the ground and that then a racial ambition for conquest led him to press out from his original arboreal home as fast and as far as he was able. But the evolutionist is confronted here with several difficulties. The dangers of life were less in the trees. Why should a species of apes court voluntarily a more hazardous life? They could not be expected to have so solved its problems that they would be better off there than those allied apes which led a more conservative and arboreal existence. Without assuming an unproved inheritance of acquired characteristics, or more logically, a forced and strenuous natural selection with survival only of the fittest, how could those considerable modifications of limb and foot structure which so differentiate man from arboreal forms have been acquired? Furthermore, it has been found in other examples that the great impulse which leads in general to new and progressive faunas and especially to the transformation of habitats is change of environment from which the organisms can not escape.

Let us turn then to the second line of explanation. The change from warm temperate forests to the more bleak conditions of the steppes must have taken place in the Miocene most markedly on the northern and interior side of the newly raised Eurasian mountain ranges. But the forest animals of this region, when their former range became restricted, could no longer freely retreat, generation by generation, to the southward. They were isolated in archipelagoes of forest in the spreading grasslands as thoroughly as the orangs are now isolated within the sea upon the islands of Sumatra and Borneo. A park-like condition of scattered groups of trees as savannahs must for ages have contested supremacy here and there with the flora of the steppes. The usual consequence of such a repressive change upon an isolated fauna is its gradual impoverishment and extermination. That small part which survives must radically change in order to meet the new conditions. In this isolation under conditions adverse for the older mode of life is found a fitting cause for the origin of man; for the apes which were trapped in this way in central Asia were forced to win most of their living on the ground. There they must have faced greater dangers, to live or die as best they might. Such a precarious life must have exercised a stern elimination of the unfit, so that only the most agile, resourceful, and cooperative were able to survive.

Let us contrast these two hypotheses of the origin of the terrestrial ape-man in some of their consequences. It is a general law, the law of parsimony, that a species does not expend energies unnecessary in its mode of life: domesticated animals tend to lose resourcefulness and hardihood; birds isolated upon oceanic islands and becoming terrestrial lose the power of flight. In contrast to this it is seen that coordinated change in several parts of an organism with resulting greater efficiency in some new and more strenuous mode of life must be forced upon organisms, and the efficient combinations of organs sifted out of chance variations by a process of natural selection. The law of probabilities declares that such a new and efficient combination of organs could not arise merely by spontaneous and orthogenetic variations in each unrelated part.

A life in tropical forests does not tend to lead moderate-sized arboreal creatures toward a terrestrial existence. On the borders of such forests or in open places a generalized form might make excursions upon the ground, but it would remain essentially arboreal and in the face especially of the powerful Tertiary fauna would have to keep the trees always in sight as a refuge, or adopt some mode of life such as seen in the ground squirrels which would protect them from their foes.

A tendency to increase in size resulting in giantism in certain species is manifested in most families of animals. A sufficient increase in size would force an arboreal animal to live partly upon the ground, since it could not leap freely through the trees. Its accompanying strength and ferocity might at last give it protection in a partly terrestrial environment, as seen in the gorilla; but this is the choosing of a retrogressive line of evolution and does not tend to rise to the intellectual level of the human plane. Rather it is a line developing away from man and toward a creature bear-like in form and habits. It does not appear then to be parallel with the course of the human ascent to a higher plane of life.

This ascent from ape to man involved a physical transformation shown in a changed foot structure, changed ratios of the limb-lengths, a changed profile of the backbone, a shortening of the jaw and a changed dentition. It involved an even greater mental transformation through which man has become set apart from all other mammals. Early man found his line of greatest efficiency in his superior mentality and through this superiority he could face his formidable adversaries. These transformations with efficiency in new modes of life could be effected most readily and perhaps only by a strenuous natural selection. The death rate must have risen and sought out unsparingly all those least able for any reason to meet the new conditions. In places the rising death rate would have led to extinction, elsewhere it spared a limited number, but these by the elimination of their non-progressive fellows had become a new kind of creature. Furthermore, separated now by geographic barriers from their nearest relatives of the trees, their hereditary strain did not tend to become submerged. Winning life by warfare waged first against them; at last successful, they carried that warfare as an offensive campaign against their terrestrial foes. From the interior Eurasian center of dispersal, man, having won efficiency upon the ground, would press out in a series of waves. *Pithecanthropus,* found in the early Pleistocene of Java, was, as shown by his femur, already far from the arboreal transformation and his location in Java has no necessary relation to the original home of man. Indeed, as Matthew has argued, the lowest forms represent the earliest migrations and are apt to be found far from the original home. In tropical forested regions and on such remote islands as he could reach, the earliest and lowest types of man have found the conditions for longest survival.

On the southern side of the Himalayas the Miocene and Pliocene faunas of the Siwaliks were forest faunas. Although the remains of a number of species and genera of primates have been found, no trace has been recovered as yet of a semi-erect, bipedal, carnivorous ape, although such, if present, would presumably have been better adapted for fossilization. If, as seems probable on other grounds, the transitional forms from ape to man were in existence at that time, they had not pressed out of their original climatic environment. As soon as they did so, on account of their dominance in numbers with increasing dominance over nature, and because of their terrestrial habitat, the chances of their leaving fossils were better than for other primates, as illustrated by the record of the Pleistocene. The Miocene ape-man may therefore be more hopefully sought in deposits of the open and temperate regions of central Asia rather than in the alluvial deposits of the more southern tropical forests.

Finally, if there be probability to this view, it contributes its weight as one of the elements of theory toward a truer philosophy of evolution. Man is seen to be not a mere product of time and life—the expression of a fancied innate tendency toward the human state—but is peculiarly a child of the earth and is born of her vicissitudes. So far as evolutionary history has been interpreted, there is found no indication that low and isolated lands with monotonous history, such as illustrated best by Australia in later geologic times, would ever have carried evolution forward to its fruition in intellectual life. Yet in the earlier Paleozoic ages the northern lands, flooded by shallow seas, were often of this character. Contrast with this geological monotony which once seemed likely to endure without end, the expansion and diversification of the land-surfaces through later geologic times, accompanied recurrently by sweeping climatic changes; that oscillation of topographic and climatic conditions which is seen to have stimulated progress.

Or again, one vast and monotonous land surface, such as is seen on the planet Mars, is not regarded as an environment well adapted to stimulate marked advances in evolution. The waves of progress have required first restriction and isolation with wide variations of conditions, so that unlike faunas could be produced and the better types acquire dominance within a limited habitat. Second, is required the migration, mingling, and competition of faunas. Judged by these principles, the post-Silurian history of the northern hemisphere is seen to have been increasingly favorable for the evolution of the higher types of land life. But that this should have been the sequence of the physical events of earth history has depended upon obscure conditions in the earth's interior which appear to have no close correspondence in the two celestial bodies whose surfaces we are able to study—the moon and Mars. The progress of life on the earth has been highly favored, consequently, by the rhythmic pulses of diastrophic and climatic changes which have remorselessly urged forward the troop of living creatures. The progress of organic evolution has depended upon a series of fortunate physical events, conditioned in the internal nature of sun and earth, rather than the byproduct of mere life activities as expressed in orthogenesis through long periods of time. Evolution is in no sense an inevitable consequence of life, and the compulsion of climatic change has been more than once a fundamental factor in the age-long ascent from protozoan to man.